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The spatial distance rule in the moving and classical rubber hand illusions



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ABSTRACT

The rubber hand illusion (RHI) is a perceptual illusion in which participants perceive a model hand as part of their own body. Here, through the use of one questionnaire experiment and two proprioceptive drift experiments, we investigated the effect of distance (12, 27.5, and 43 cm) in the vertical plane on both the moving and classical RHI. In both versions of the illusion, we found an effect of distance on ownership of the rubber hand for both measures tested. Our results further suggested that the moving RHI might follow a narrower spatial rule. Finally, whereas ownership of the moving rubber hand was affected by distance, this was not the case for agency, which was present at all distances tested. In sum, the present results generalize the spatial distance rule in terms of ownership to the vertical plane of space and demonstrate that also the moving RHI obeys this rule.

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1. Introduction

In the rubber hand illusion, participants perceive a model hand as part of their own body (Botvinick & Cohen, 1998). This bodily illusion can be induced by touching the rubber hand, which is presented in full view in front of the participant, in synchrony with touches applied to the participant's hand, which is hidden from view behind a screen. When experiencing this visual and tactile stimulation for a short period, sometimes even less than 10 s, the majority of participants starts to sense the touch as originating from the model hand (referral of touch) and experience that the rubber hand feels like their own hand (sense of ownership). To understand the basic processes that mediate this illusion (and thereby, learning something about how body self-perception works under more natural conditions), it is important to identify the basic rules that determine this illusion. Thus, several studies have set out to identify the basic constraints that govern the rubber hand illusion. These studies have shown that visual and tactile stimulation must occur in synchrony (Botvinick & Cohen, 1998; Ehrsson, Spence, & Passingham, 2004; Tsakiris & Haggard, 2005), in the same direction (Costantini & Haggard, 2007; Gentile, Guterstam, Brozzoli, & Ehrsson, 2013) and sufficiently close in space (Lloyd, 2007) for the illusion to be elicited. If the visuo-tactile stimulation is applied asynchronously, if it is applied in opposing directions on the hands, or if the visually stimulated rubber hand is placed far from the participant's hand, then the illusion is not elicited. Moreover, the model hand must be placed in an anatomically plausible position that matches the posture of the real hand (Ehrsson et al., 2004; Ide, 2013; Tsakiris & Haggard, 2005). All of these findings fit well within a theoretical framework in which body-self perception arises as a consequence of multisensory integration and continuous dynamic updating of the central body representation (Ehrsson, 2012; Graziano & Botvinick, 2002).

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In previous literature, there are relatively few studies that have examined the spatial constraints of the rubber hand illusion. This is particularly surprising given the importance of this constraint to the question of the kind of process that is responsible for the illusion. For example, [Lloyd \(2007\)](#) found that the strength of the illusion, as measured by a subjective rating of the illusion (referral of touch), decreases significantly when the rubber hand is placed more than 27.5 cm away from the participant's hand. [Zopf, Savage, and Williams \(2009\)](#) re-examined the effect of distance and found somewhat mixed results, whereby the illusion appeared to be inducible at a distance of 45 cm. [Armeli and Ramachandran \(2003\)](#) claimed that the illusion could be elicited beyond the participant's reaching space and at a distance of 91 cm from the participant; however, their questionnaire data actually suggested a substantial reduction of the effect at this distance. More recently, [Preston \(2013\)](#) found that the absolute distance between the rubber hand and the participant's hand, as well as the distance of the model hand relative to the participant's trunk and whether the model hand is placed laterally or medially in regard to the participant's hand, matters. All these previous studies investigated the effect of distance in the horizontal plane so we do not know if the effect holds true in other planes of space. Demonstrating a generalization of this rule to a different plane of space would support the view that the spatial distance rule corresponds to a fundamental principle determining the illusion.

Recently, we introduced a version of the rubber hand illusion that was based on finger movement instead of externally applied touches. In this version, the participant moves his or her finger and the model hand's finger either moves synchronously or asynchronously with respect to the participant's movements ([Kalckert & Ehrsson, 2012](#)). When the movements of the participant's finger and the model's finger are synchronous, participants report a vivid feeling of ownership of the model hand and report experiencing somatic sensations from the location where they see the model finger move (see also, [Dummer, Picot-Annand, Neal, & Moore, 2009](#); [Sanchez-Vives, Spanlang, Frisoli, Bergamasco, & Slater, 2010](#); [Tsakiris, Prabhu, & Haggard, 2006](#)). This illusion seems to work equally well for active and passive finger movements ([Kalckert & Ehrsson, 2012, 2014](#); [Tsakiris et al., 2006](#)), although in the case of active movements, the participants also experience a strong sense of agency ([David, Newen, & Vogeley, 2008](#); [Jeannerod, 2003](#)), that is, the sense of being the one to generate the model's finger movements ([Kalckert & Ehrsson, 2012](#)). In the moving rubber hand illusion paradigm, the ownership-illusion effect is elicited by matching somatosensory and visual feedback from the fingers. Sense of agency, by contrast, arises as a consequence of the match between the intention to move and the visual and somatosensory feedback from the model hand that matches those intentions ([Kalckert & Ehrsson, 2012](#)). Despite the procedural differences and differences in the types of somatosensory submodalities involved with respect to the classical version, the moving rubber hand illusion seems to involve a highly similar illusory experience of owning the model hand. This is reflected in high questionnaire ratings of ownership and a significant proprioceptive drift toward to model hand, which quantifies the degree to which participants experience their hand to be closer to the model's hand ([Kalckert & Ehrsson, 2012](#); [Riemer, Kleinbühl, Hölzl, & Trojan, 2013](#); [Tsakiris et al., 2006](#)). Moreover, when testing the classical rubber hand illusion and the moving rubber hand illusion with the same group of participants, these measures were correlated, indicating that the strength of the moving rubber hand illusion can be predicted from the strength of the classical illusion ([Kalckert & Ehrsson, 2014](#)). When violating the temporal synchronicity of the seen and felt finger movements ([Dummer et al., 2009](#); [Tsakiris et al., 2006](#)) or the anatomical plausibility of the model hand ([Kalckert & Ehrsson, 2012](#); [Tsakiris & Haggard, 2005](#)), the rubber hand illusion is not induced, which is consistent with the rules of the classical version of the illusion. However, the important question of whether the spatial distance rule also applies to the moving rubber hand illusion has not yet been investigated. Demonstrating this would support the hypothesis that the moving rubber hand illusion obeys the same fundamental constraints as the classical rubber hand illusion, which in turn would suggest the involvement of similar multisensory processes ([Ehrsson, 2012](#); [Kalckert & Ehrsson, 2012](#)).

In the present study, we compare the moving (visuo-motor) and classical (visuo-tactile) versions of the rubber hand illusion by using different distances between the model hand and the participant's hand (12, 27.5, and 43 cm) in the vertical plane. In particular, we are testing the hypothesis that the moving rubber hand illusion will obey a spatial rule that is similar to that of the classical illusion, which means that we expect to find a diminishing effect of the illusion when the hands are further apart. Second, we expect to find an effect of spatial distance for the sense of ownership, but we do not expect to find this effect for the sense of agency. This hypothesis is grounded in the notion that only ownership will depend on the multisensory integration of body-part centered spatial reference frames ([Ehrsson, 2012](#)), thereby restricting the model hand to a space near the hand within one's peripersonal space ([Brozzoli, Ehrsson, & Farnè, 2013](#)). However, agency involves a process of matching motor intention to sensory feedback that is not expected to be constrained to the body or to a space near a body part ([Kalckert & Ehrsson, 2012](#)).

2. Methods and results

2.1. General procedures

Participants sat on a chair next to a table on which a wooden box with the measures of 30 × 20 × 12 cm had been placed. A life-size, wooden model of a right hand was placed on top of the box in the participant's direct view. The box onto which the model hand was placed was freely movable along the vertical axis and could, thus, easily be positioned at different heights. The participant's right hand was underneath the box and on the table (see [Fig. 1](#)). The model hand measured 20 cm in length (from wrist end to the tip of the middle finger) and was covered with a latex glove. Participants wore

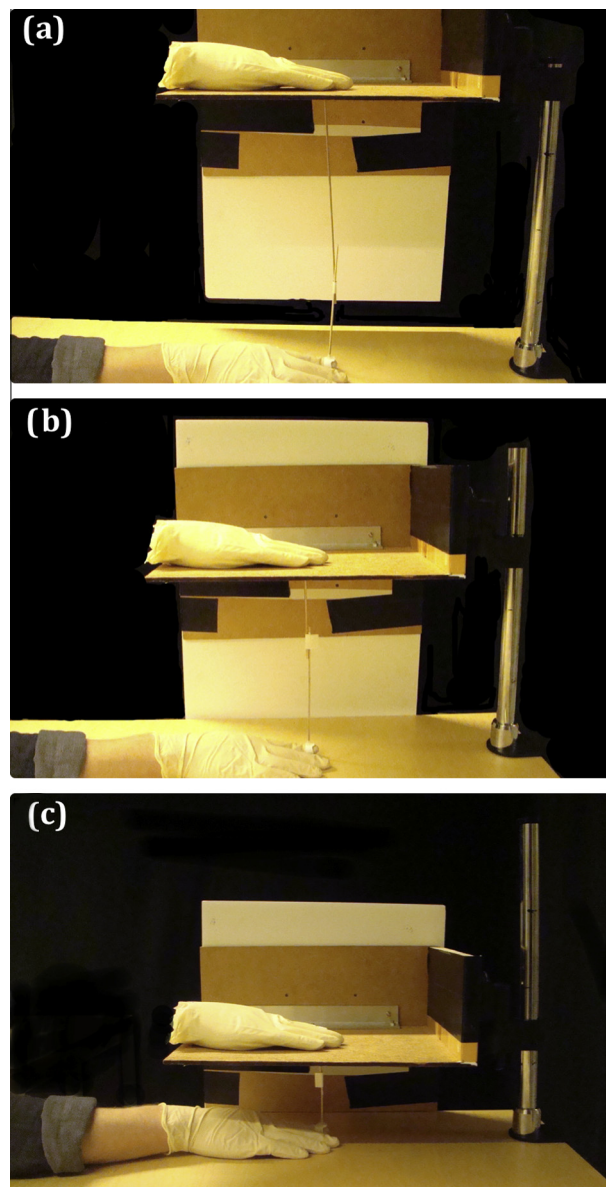


Fig. 1. Illustration of the setup: the model hand was placed on a platform with an adjustable height ($a = 43$ cm, $b = 27.5$ cm and $c = 12$ cm). The participant's hand rested on the table below the platform (note that both hands were fitted with identical latex gloves). The distance of 12 cm is identical to our previous experiments (see Kalckert and Ehrsson, 2012, 2014). In the moving rubber hand illusion conditions, the two hands were mechanically connected with a light stick, and in the classical rubber hand illusion conditions, there was no connection, and the participant received brush strokes on the finger instead. Please note that in this figure, the cloth that normally covered the participant's right arm to hide it from view was removed to illustrate the spatial arrangement of the hands and the mechanical connection.

identical latex gloves on their right hands. A blanket was placed over the participant's right shoulder to cover the space between the model hand and the participant, which was meant to aid the participant's perception of the model hand actually being the participant's own outstretched right hand. With this arrangement, we could, thus, examine the effect of changing the distance between the hands in the rubber hand illusion that was induced by visuo-motor and visuo-tactile correlations.

In the moving rubber hand illusion conditions, the participant's index finger was connected to the model hand by a light wooden stick that was attached to a ring worn on the participant's fingertip (see Kalckert & Ehrsson, 2012). For each of the three distances tested, a mechanical connection of different lengths was used. The participant had been instructed and trained to execute repetitive index finger taps (extension movements) at a pace of approximately 1 Hz. When the mechanical connection between the stick and the ring was locked, the model hand moved in perfect synchrony with the participant's own finger movements. In the asynchronous condition, the mechanical coupling was unlocked, and the experimenter,

who was sitting across from the participant, moved the finger of the model hand by pulling on the unlocked wooden stick in the box. The experimenter's arm and hand that were operating the sticks and generating the model finger movements were hidden under a cover so that the participant could not see the experimenter move the model index finger. The experimenter was sitting across from the participant and the box in all of the conditions.

In the classical illusion conditions, the participants' right index finger and the model hand's index finger were stroked with two small brushes that touched the proximal phalanx of the finger. These touches were delivered at a frequency of 1 Hz either synchronously (in the illusion condition) or asynchronously (in the control condition) (Botvinick & Cohen, 1998). Thus, the total number of seen and felt sensory events was matched across the synchronous and asynchronous conditions and across the moving and classical versions of the illusions (also, see Kalckert & Ehrsson, 2014). In all of the conditions, the participants were instructed to sit still and focus their gaze on the index finger of the model hand.

3. Experiment 1

3.1. Methods – Experiment 1

In Experiment 1, we tested a group of 40 participants (23 females, age range: 18–38, mean age: 24.2 years). We tested three different distances: 12 cm (which is identical to our previous experiments, see Kalckert & Ehrsson, 2012, 2014), 27.5 cm (which is identical to the spatial limit found in a previous study by Lloyd, 2007) and 43 cm (which is similar to the distance used in the study by Zopf et al., 2009; 45 cm in Experiment 2), so the distances increase by 15.5 cm. The choice of the furthest distance was also constrained by the fact that we could not position the box higher without making it difficult for the participant to be able to see the model hand.

In a $2 \times 2 \times 3$ factorial design, we varied the following factors: Induction type (Moving, Classical), Timing (Synchronous, Asynchronous) and distance (close: 12 cm, medium: 27.5 cm, far: 43 cm), resulting in 12 different conditions. Trial order was pseudo-randomized and balanced across participants. Each condition lasted 90 s, after which the participant rated each item on a questionnaire regarding their experience on a 7-point Likert scale (+3: totally agree; –3: totally disagree; with 0 indicating uncertainty). The questionnaire consisted of three statements related to sense of ownership and three statements related to sense of agency. We also included six control statements, three serving as controls for ownership and three serving as controls for agency, that were meant to control for task compliance and suggestibility effects. The statements in the agency category differ from the initial study (Kalckert & Ehrsson, 2012) because they had to be reformulated to be applicable to both the moving and the non-moving classical rubber hand illusions (see Kalckert & Ehrsson, 2014) (see Table 1).

We averaged the three statements for each category, which resulted in four different scores: ownership rating, ownership control rating, agency rating, and agency control rating. In the following section, we compare these ratings and evaluate whether significant differences can be found by using Friedman or Wilcoxon tests for the questionnaire data. As in previous studies, we interpret a category as rated positively, or affirmed, when the group median score is equal to or higher than +1, meaning that the majority of participants gave a positive rating of the individual category. When an ownership rating or an agency rating is affirmed, we then move on to a more detailed statistical analysis that will allow us to look for significant differences in regard to the control ratings and the control conditions. We first statistically compare the ratings on the ownership or agency categories to their respective control ratings. Then, we compare the ownership or agency category ratings directly across conditions by comparing the synchronous conditions to the asynchronous conditions, the latter serves as a control condition. Reported statistical results are two-tailed, if not otherwise stated. An overview of the results can be seen in Table 2 and Fig. 2.

3.2. Results – Experiment 1

3.2.1. Moving rubber hand illusion

12 cm Distance: As expected, after synchronous movements, participants gave high ratings of ownership (Median: 1.7) and agency (Median: 2.7) and clearly affirmed both of these categories (≥ 1). The ownership category was significantly different from its control category in the synchronous conditions (Ownership Synchronous vs. Ownership Control Synchronous: $Z = -5.063$, $p < .001$) and also significantly higher during synchronous rather than asynchronous movements (Ownership Synchronous vs. Ownership Asynchronous: $Z = -5.180$, $p < .001$). Participants' rating of agency during synchronous movements was significantly higher than it was during asynchronous movements (Agency Synchronous vs. Agency Asynchronous: $Z = -4.341$, $p < .001$), and it was also significantly higher than it was during the control category (Agency Synchronous vs. Agency Control Synchronous: $Z = -5.496$, $p < .001$). During asynchronous movements, the ownership category was rated negatively (Median: –1.33), and the agency category had slightly positive ratings (Median: 0.7). In summary, participants experienced both a sense of ownership and a sense of agency over the model hand when the hand moved synchronously and at a position that was 12 cm above the participant's hand.

27.5 cm Distance: After synchronous movements, participants did not affirm the ownership statements when the model hand was placed at the intermediate distance of 27.5 cm (Median: 0.3). Nevertheless, the agency category was affirmed at this distance (Median: 1.8) and was significantly higher than its control category (Agency Synchronous vs. Agency Control Synchronous: $Z = -5.405$, $p < .001$), but the synchronous condition was not significantly higher than the asynchronous

Table 1

Statements used in the questionnaire.

Ownership	1	I felt as if I was looking at my own hand
	2	I felt as if the rubber hand was part of my body
	3	I felt as if the rubber hand was my hand
Ownership control	1	It seems as if I had more than one right hand
	2	It felt as if I had no longer a right hand, as if my right hand had disappeared
	3	I felt as if my real hand was turning rubbery
Agency	1	I felt as if I could cause movements of the rubber hand
	2	I felt as if I could control movements of the rubber hand
	3	The rubber hand was obeying my will and I can make it move just like I want it
Agency control	1	I felt as if the rubber hand was controlling my will
	2	It seemed as if the rubber hand had a will of its own
	3	I felt as if the rubber hand was controlling me

Table 2

Median values and percentiles of each rating in all 12 conditions.

	Synchronous				Asynchronous			
	Ownership	Ownership control	Agency	Agency control	Ownership	Ownership control	Agency	Agency control
Moving RHI								
12 cm								
Median	1.7	−1.0	2.7	−2.8	−1.3	−1.0	0.7	−1.7
Percentiles								
25	0.0	−2.3	1.7	−3.0	−2.7	−2.9	−0.3	−2.6
75	2.6	0.6	3.0	−1.8	0.3	−0.1	2.0	−0.7
27 cm								
Median	0.3	−1.3	1.8	−2.7	−1.3	−1.3	1.3	−2.0
Percentiles								
25	−0.9	−2.9	0.7	−3.0	−3.0	−3.0	0.0	−2.7
75	1.3	−0.3	2.6	−1.7	−0.1	−0.8	2.0	−1.0
43 cm								
Median	0.3	−1.7	2.5	−2.7	−1.5	−1.8	0.8	−2.0
Percentiles								
25	−2.3	−2.7	1.4	−3.0	−3.0	−3.0	0.0	−2.7
75	1.9	0.0	3.0	−1.4	0.2	−0.7	1.3	−0.8
Classical RHI								
12 cm								
Median	1.7	−1.3	−1.0	−1.8	−0.7	−1.3	−1.3	−1.7
Percentiles								
25	0.1	−2.3	−2.3	−3.0	−2.0	−2.7	−3.0	−3.0
75	2.3	−0.1	0.9	−0.4	0.9	0.5	0.0	−1.0
27 cm								
Median	1.2	−1.2	−0.3	−2.0	−2.2	−2.3	−2.3	−2.0
Percentiles								
25	−0.3	−2.3	−2.6	−3.0	−3.0	−3.0	−3.0	−3.0
75	2.0	0.3	0.9	−1.1	−1.0	−0.4	−1.0	−0.8
43 cm								
Median	0.2	−1.0	−1.2	−2.0	−2.3	−2.0	−2.3	−2.0
Percentiles								
25	−1.3	−2.7	−2.9	−3.0	−3.0	−3.0	−3.0	−3.0
75	1.0	0.0	0.6	−0.8	−0.7	−0.4	−1.3	−1.0

condition (Agency Synchronous vs. Agency Asynchronous: $Z = -1.498$, $p = .134$). Additionally, the agency rating in the asynchronous condition was affirmed (Median: 1.3) and was significantly higher than its control category (Agency Asynchronous vs. Agency Control Asynchronous: $Z = -5.405$, $p < .001$). Thus, at the intermediate distance of 27 cm, participants were uncertain about what extent the hands felt as if they were their own, but the participants affirmed agency of the finger movements.

43 cm Distance: Participants did not affirm the ownership category of statements at this distance (Median: 0.3). The agency category was affirmed during synchronous movements (Median: 2.5), and this category was significantly higher than the control category (Agency Synchronous vs. Agency Control Synchronous: $Z = -5.440$, $p < .001$) and the agency category during asynchronous movements (Agency Synchronous vs. Agency Asynchronous: $Z = -4.700$, $p < .001$). Thus, participants experienced a sense of agency, but they did not experience ownership at the furthest distance.

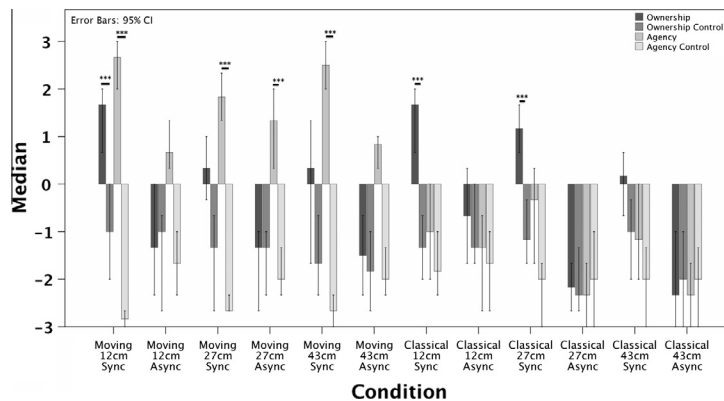


Fig. 2. Ratings of ownership, ownership control, agency, and agency control in all of the tested conditions of Experiment 1. In the cases where the median rating exceeded +1, indicating that ownership or agency was affirmed, we statistically compared these ratings to the ratings on the respective control statements or control condition. Asterisks indicate the level of significance: *** $p < .001$.

3.2.2. Classical rubber hand illusion

12 cm Distance: As expected, participants affirmed the ownership category (Median: 1.7), but they did not affirm the agency category (Median: -1.0), during synchronous stimulation at this distance. The ownership category was significantly higher than the control category (Ownership Synchronous vs. Ownership Control Synchronous: $Z = -5.104$, $p < .001$) and higher than in the asynchronous stimulation condition (Ownership Synchronous vs. Ownership Asynchronous: $Z = -4.312$, $p < .001$). Therefore, when the hand was stimulated with synchronous brush strokes, participants felt strong ownership over the hand at the 12 cm distance, which most closely matches the distance that is typically used in the classical version of this paradigm.

27.5 cm Distance: At the intermediate distance, the participants affirmed the ownership category of statements in the synchronous condition (Median: 1.2), but they did not affirm agency in this condition (Median: -0.3). Similarly, this ownership category was rated significantly higher than its control category (Ownership Synchronous vs. Ownership Control Synchronous: $Z = -4.898$, $p < .001$) and the ownership category in the asynchronous condition (Ownership Synchronous vs. Ownership Asynchronous: $Z = -5.175$, $p < .001$). Thus, at the intermediate distance of 27.5 cm, participants feel a sense of ownership over the model hand in the synchronous condition, but not in the asynchronous condition, just as they had felt at the closer distance of 12 cm (see above).

43 cm Distance: At the furthest distance, neither the ownership category (Median: 0.2) nor the agency category (Median: -1.2) was affirmed in the synchronous condition. Thus, no explicit illusion of ownership or sense of agency over the hand was reported by the participants. Consequently, no further statistical comparisons were conducted.

3.2.3. Number of illusion responders

We calculated the number of responders to the illusion by using a cut-off score of $\geq +1$ in regard to the ownership rating (Kalckert & Ehrsson, 2012; Petkova & Ehrsson, 2009).

For the moving rubber hand illusion at the 12 cm distance, 26 participants (65%) were classified as responders; at the 27.5 cm distance, 16 participants (40%) belonged to this group; and at the 43 cm distance, 19 participants (47.5%) responded to the illusion. In the classical rubber hand illusion, we observed at the 12 cm distance that 25 participants (62.5%) were classified as responders, at the 27.5 cm distance that 25 participants (62.5%) were responders, and at the 43 cm distance that 13 participants were illusion responders (32.5%).

3.2.4. Ownership at different distances

To determine whether distance affects one's sense of ownership, we compared the ownership ratings of the three synchronous conditions by using a Friedmann test. Additionally, we performed pairwise comparisons by using a Wilcoxon test. Further, based on the number of ownership responders (Ownership category ≥ 1), we compared the three synchronous conditions by using a McNemar test to determine whether the number of responders significantly differs at the three distances within each induction type and also between the moving and classical rubber hand illusions.

When comparing the ownership ratings of the three synchronous conditions of the moving rubber hand illusion, we observed that these significantly differed from one another ($\chi^2 = 23.755$, $df = 2$, $p < .001$). When performing pairwise comparisons, we observed significantly greater affirmative ratings in the 12 cm condition than in the 27.5 cm condition ($Z = -3.950$, $p < .001$) or in the 43 cm condition ($Z = -4.539$, $p < .001$). The 27.5 cm and 43 cm conditions did not differ in terms of ownership ratings ($Z = -0.821$, $p = .412$) (see Fig. 3). We obtained a similar pattern of results when we analyzed the number of responders at the three different distances: the 12 cm condition had significantly more responders than the 27.5 cm condition ($n = 40$, $p = .006$) or the 43 cm condition ($n = 40$, $p = .039$); however, the latter two distances did not differ from each other in terms of the number of responders ($n = 40$, $p = .581$).

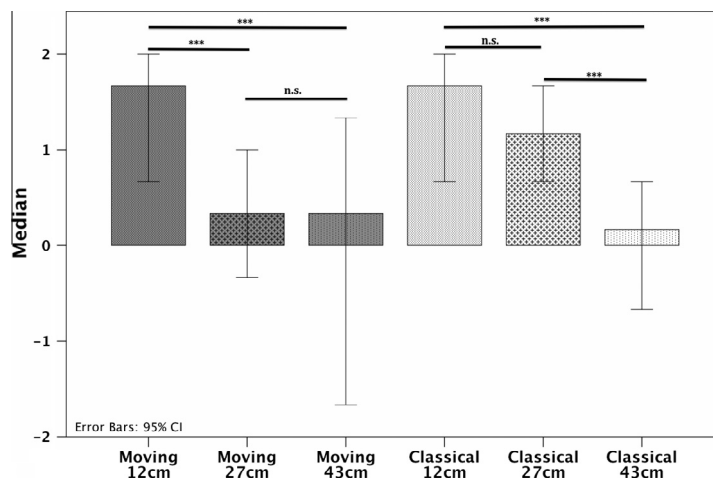


Fig. 3. Ownership ratings in the synchronous conditions at the three distances. For the moving rubber hand illusion, a high ownership rating can be seen at the 12 cm distance, but not at the other distances. For the classical rubber hand illusion, we see affirmative ratings at the 12 cm distance and the 27.5 cm distance (albeit smaller), but not at the 43 cm distance.

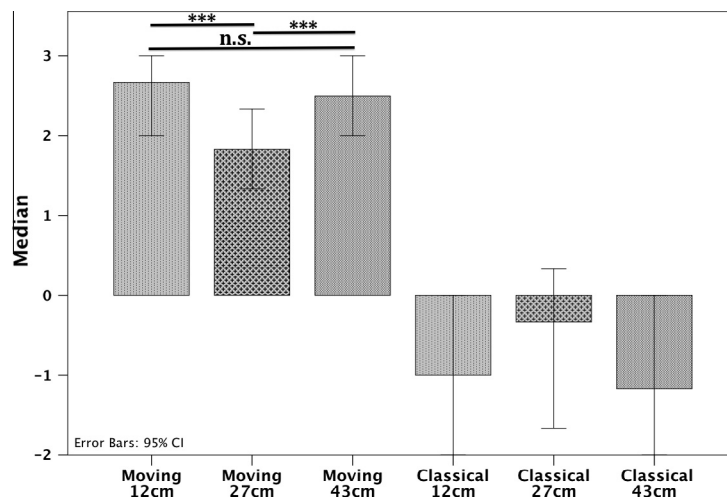


Fig. 4. Agency ratings in the synchronous conditions at the three distances: agency ratings were only high for the moving rubber hand illusion conditions. They were not high for the classical conditions.

When we compared the ownership ratings of the three synchronous conditions of the classical rubber hand illusion, we observed that these significantly differed from one another ($\chi^2 = 21.257$, $df = 2$, $p < .001$). In contrast to what we noted for the moving rubber hand illusion conditions (see above), the 12 cm condition did not significantly differ from the 27.5 cm condition in terms of rated ownership ($Z = -1.705$, $p = .088$), but it was associated with significantly greater ownership than the 43 cm condition ($Z = -4.234$, $p < .001$). Additionally, the 27.5 cm condition was associated with significantly greater ownership ratings than the 43 cm condition ($Z = -3.238$, $p < .001$). We observed a similar pattern of results when we analyzed the number of ownership illusion responders with a McNemar test: there was no significant difference between the 12 cm and 27.5 cm conditions ($n = 40$, $p = 1.000$); however, there were significantly more ownership-illusion responders at the 12 cm distance than at the 43 cm distance ($n = 40$, $p < .001$), and they were significantly more responders at 27.5 cm than at 43 cm ($n = 40$, $p = .002$).

3.2.5. Agency at different distances

A sense of agency was reported by the participants in the moving rubber hand illusion, but it was not reported in the classical version of the illusion. At all three distances, participants gave high affirmative ratings of agency in the synchronous conditions, which was in line with our expectations (Median ratings at 12 cm: 2.7, at 27.5 cm: 1.8, at 43 cm: 2.5) (see Fig. 4). The agency ratings in the classical rubber hand illusion conditions were all below zero, thus participants did not affirm agency in any of these conditions (Median ratings at 12 cm: -1.0, at 27.5 cm: -0.3, at 43 cm: -1.2). This is expected because

no voluntary movements are executed in the classical version of the illusion, and voluntary motor commands are considered to be essential in regard to agency of bodily movements (Kalckert & Ehrsson, 2012).

Next, we compared the agency ratings in the synchronous conditions at the three distances and found, to our surprise, a significant difference between these ($\chi^2 = 18.786$, $df = 2$, $p < .001$). When we compared the individual conditions, we found that this difference was expressed both when comparing the 12 cm and 27 cm distances ($Z = -4.044$, $p < .001$) and the 27.5 cm and 43 cm distances ($Z = -3.215$, $p < .001$), but no difference was found between the 12 cm and 43 cm conditions ($Z = -0.551$, $p = .582$). This unexpected difference seems to be rooted in the relatively lower affirmative agency ratings in the 27.5 cm condition (Median: 1.8, compared to 2.7 at 12 cm and 2.5 at 43 cm). Thus, this unexpected “drop” in agency at the intermediate distance seems to drive the significant overall difference across the conditions that we observed. We do not have any theoretically motivated expectation for this incidental finding: if distance is genuinely affecting agency, then one would expect a diminished agency for the 43 cm distance rather than the 27.5 cm distance. Importantly, there was no statistically significant difference in agency between the 12 cm and 43 cm distance conditions.

3.2.6. Comparing the moving and classical rubber hand illusions at different distances

Ownership: Next, we compared the strength of ownership between the moving and classical rubber hand illusions across the three distances. The two versions of the rubber hand illusion did not differ in terms of rated ownership at the 12 cm distance ($Z = -.423$, $p = .672$) or the 43 cm distance ($Z = -.231$, $p = .817$), but we observed a statistical trend at 27.5 cm ($Z = -1.875$, $p = .061$). Similarly, the McNemar test shows that both induction types of the rubber hand illusion did not differ in terms of illusion responders at 12 cm ($n = 40$, $p = 1.000$) or at 43 cm ($n = 40$, $p = .210$), but at the 27.5 cm distance, a significant difference in responders was noted, with relatively fewer responders in the moving condition ($n = 40$, $p = .049$).

Agency: Similarly, we compared the agency ratings of the synchronous moving and classical rubber hand illusions at the three distances and unsurprisingly found that there is a significant difference between the two induction types. The agency ratings were always higher in the moving rubber hand illusion than in the classical illusion (Ownership Moving vs. Ownership Classical at 12 cm: $Z = -4.898$, $p < .001$; at 27.5 cm: $Z = -4.344$, $p < .001$; at 43 cm: $Z = -5.415$, $p < .001$). This is, of course, not surprising given that voluntary movements are only produced in the moving rubber hand illusion paradigm.

3.2.7. Correlations of ownership ratings between induction types

We then moved on to test whether ownership ratings correlate between the moving and classical illusions at each distance. If this were to be the case, then this would further strengthen the evidence for similar processes being involved in both versions of the illusion. At the 12 cm distance, ownership ratings between the moving and classical versions of the illusion correlated significantly (Spearman: $r = .611$, $n = 40$, $p < .001$), and at the 27.5 cm distance, the correlation was also significant (Spearman: $r = .347$, $n = 40$, $p = .028$). At the 43 cm distance, the correlation was not significant, although a statistical trend was observed (Spearman: $r = .292$, $n = 40$, $p = .067$) (see Fig. 5). Thus, individuals who experience a strong moving rubber hand illusion also tend to be those who experience a strong classical rubber hand illusion.

3.2.8. Correlations of ownership ratings across distances

We further tested whether the strength of the illusion at the closest distances could be used to predict the ratings of ownership at the two further distances. The rationale here is that a person who displays a vivid illusion at the closest distance should be expected to report a stronger illusion at the intermediate distance than a person who reported a weak illusion at the closest distance. To examine this, we performed correlations (Spearman) between ownership ratings of the 12 cm condition and the 27.5 cm condition and of the 12 cm condition and the 43 cm condition, respectively.

For the moving rubber hand illusion conditions, we observed a highly significant correlation between the ownership rating of the 12 cm condition and the 27.5 cm condition (Spearman: $r = .678$, $n = 40$, $p < .001$), as well as between the 12 cm condition and the 43 cm condition (Spearman: $r = .720$, $n = 40$, $p < .001$). Likewise, we observed, for the classical illusion conditions, a high correlation between the 12 cm condition and the 27.5 cm condition (Spearman: $r = .699$, $n = 40$, $p < .001$) and between the 12 cm condition and the 43 cm condition (Spearman: $r = .640$, $n = 40$, $p < .001$). Thus, participants who responded strongly to the stimulation at the closest distance also showed a relatively strong response at the further distances (see Fig. 6).

4. Experiment 2

4.1. Methods – Experiment 2

In the second experiment, we tested 15 participants (8 females, mean age: 28.3 years, range: 19–43 years) on the proprioceptive drift test, which serves as an objective measure of the rubber hand illusion when comparing synchronous and asynchronous conditions (Kalckert & Ehrsson, 2012; Tsakiris et al., 2006). In a 2×2 factorial design, we compared the 12 cm and the 27.5 cm distance conditions with synchronous and asynchronous feedback. We expected for the proprioceptive drift result to mirror the results that were obtained in the questionnaire experiment described above. Thus, we predicted a significant difference of drift between the synchronous condition and the asynchronous condition for the 12 cm condition, but not for the 27.5 cm condition, as participants did not affirm the moving rubber hand illusion at this distance (see Experiment 1).

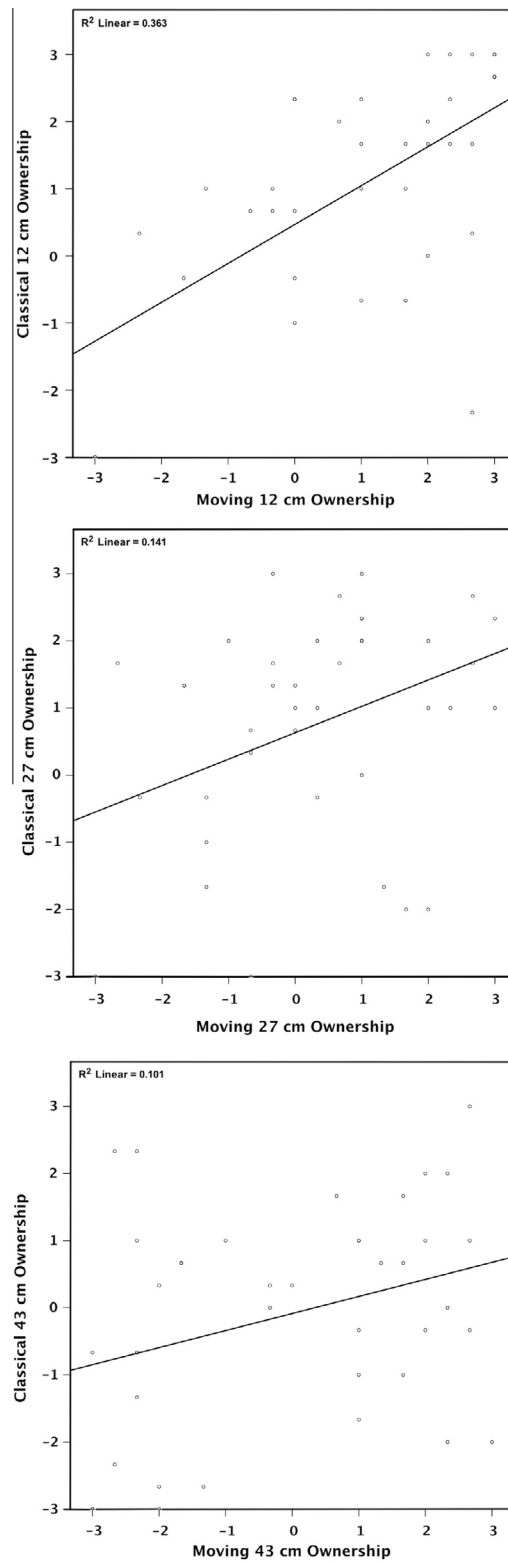


Fig. 5. Correlations between the moving and classical rubber hand illusion at each of three distances. At 12 cm and 27.5 distance a significant correlation was found ($p < .05$), at 43 cm a trend ($p = .067$).

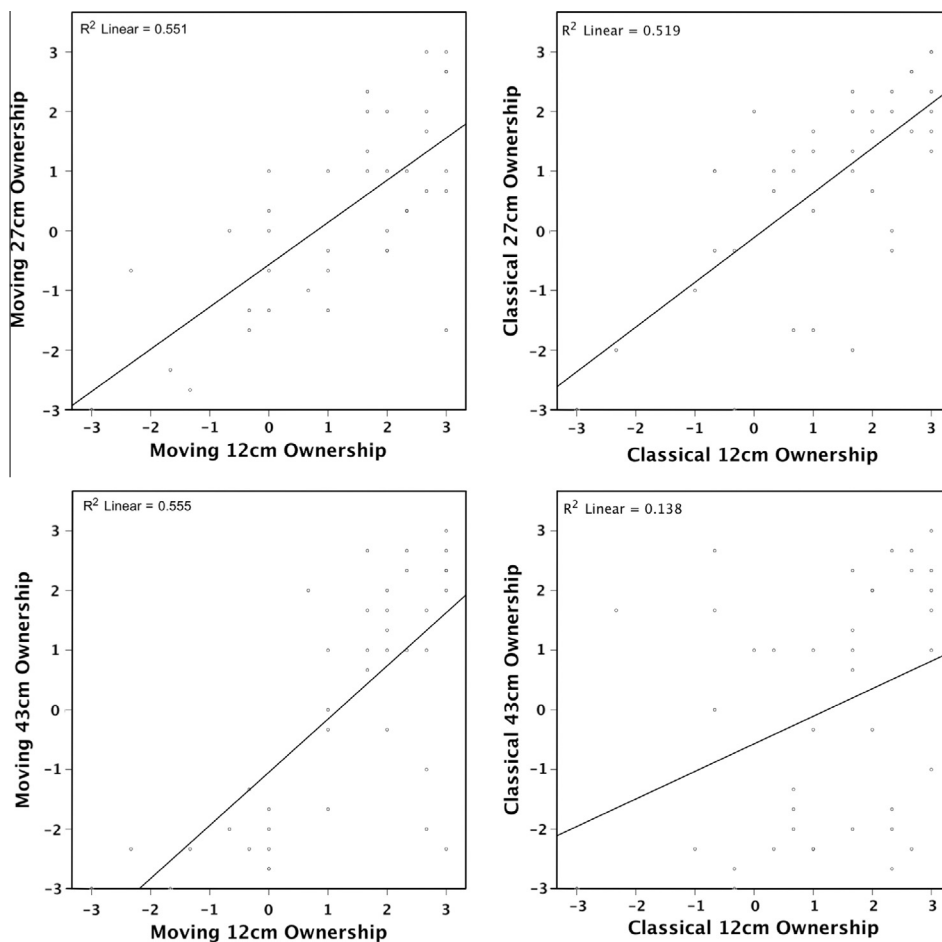


Fig. 6. Significant correlations ($p < .05$) of ownership ratings at different distances: for both the moving and the classical rubber hand illusions, ownership ratings at the closest distance highly correlate with ownership ratings at the further distances.

Participants were instructed to point with the left index finger to the felt position of their right finger along the vertical axis before (pre-pointing) and after (post-pointing) the 90 s illusion induction period regarding finger movements. Pointing movements were always executed with the eyes closed. We then subtracted the pre-pointing position from the post-pointing position in order to obtain a drift score. Each of the four conditions (Synchronous 12 cm, Asynchronous 12 cm, Synchronous 27.5 cm, and Asynchronous 27.5 cm) was repeated three times, resulting in 12 trials in total. We averaged the three drift scores that were obtained from each condition; a positive score indicates a drift toward the model hand. Trial order was pseudo-randomized and balanced across participants. The data were tested for normality through the use of a Shapiro–Wilk test and was normally distributed ($p > .05$).

4.2. Results – Experiment 2

The results of the proprioceptive drift experiment are summarized in Fig. 6. A difference in drift toward the model hand (by comparing the synchronous and asynchronous conditions) was only observed at the closest distance (12 cm). In the statistical analysis, we entered the drift values into an ANOVA and found a significant effect of distance ($F(1,14) = 6.047$, $p = .028$) and a significant effect of timing ($F(1,1) = 5.086$, $p = .041$), with the interaction showing a strong trend toward significance ($F(1,14) = 4.549$, $p = .051$). We also recalculated the absolute drift values into relative drift values in terms of the percentage of the actual distance between the subject's hand and the model hand, which is a better way to compare differences in the amount of proprioceptive drift across different distances between the hands (see Preston, 2013). In this analysis, we found a significant main effect of timing ($F(1,14) = 8.194$, $p = .013$), a statistically significant main effect of distance ($F(1,14) = 5.738$, $p = .031$), and a significant interaction between timing and distance ($F(1,14) = 8.932$, $p = .010$). When calculating individual pairwise comparisons, we found significantly greater proprioceptive drift in the synchronous condition than in the asynchronous condition at the 12 cm distance ($t = 3.217$, $df = 14$, $p = .006$), but not at the 27 cm distance

($t = 0.383$, $df = 14$, $p = .707$). In sum, the drift results suggest that illusion-related proprioceptive drift toward the model hand is present at the 12 cm distance rather than the 27 cm distance (Fig. 7a).

5. Experiment 3

5.1. Methods – Experiment 3

In Experiment 3, we repeated the experimental procedure of Experiment 2, but we examined the classical rubber hand illusion in 15 new participants (12 female, mean age: 29.7 years, range: 21–41 years). The results of Experiment 1 suggested that the classical rubber hand illusion could be induced at both the 12 cm and the 27.5 cm distances. In line with this observation, we expected significantly greater drift in the synchronous simulation than in the asynchronous simulation, at both distances (12 cm and 27.5 cm). Furthermore, the classical version of the rubber hand illusion has not been tested at varying vertical distances between the hands (Lloyd, 2007; Preston, 2013; Zopf et al., 2009). Thus, it was important to test the spatial distance rule in the vertical plane by using the proprioceptive drift test in the classical illusion paradigm.

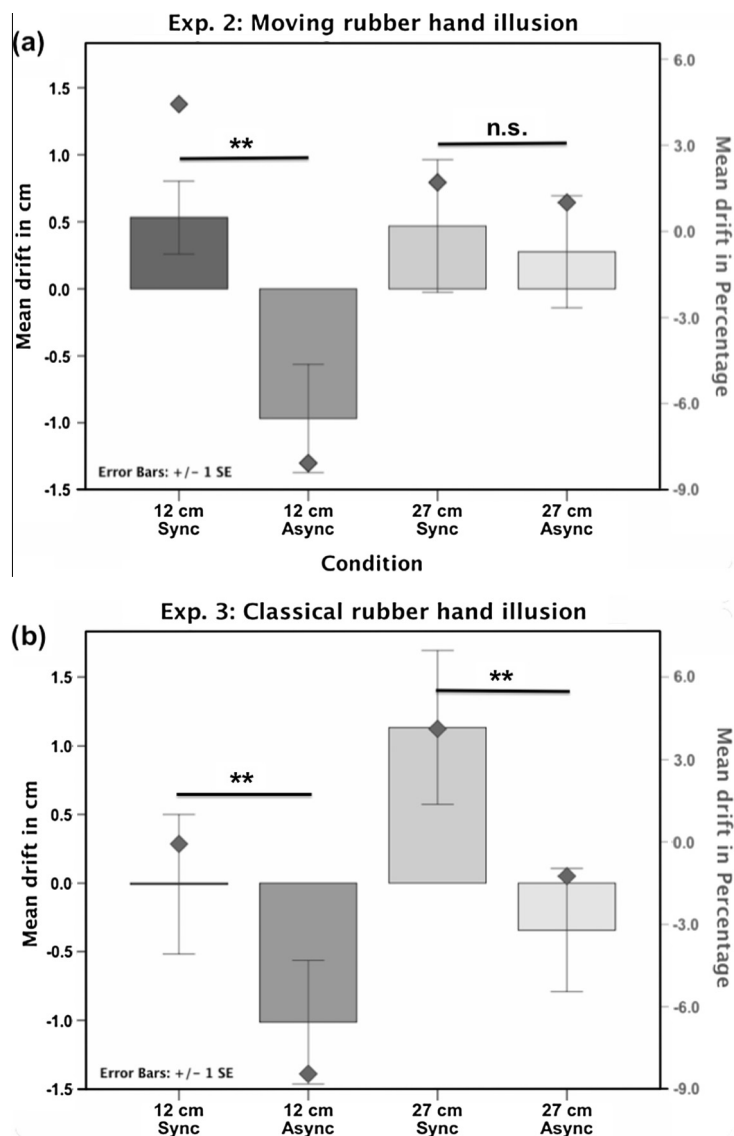


Fig. 7. Results of the proprioceptive drift experiments 2 and 3: (a) Moving rubber hand illusion: a significant difference between the synchronous and asynchronous conditions is present at 12 cm, but not 27.5 cm. (b) Classical rubber hand illusion: significant differences between the synchronous and asynchronous conditions are present at both the 12 cm and the 27.5 cm distances. The diamonds indicate the mean value of the drift as a percentage of the distance between the two hands (right x-axis).

5.2. Results – Experiment 3

We analyzed the data in the same way that it was done in Experiment 2. We entered the drift values into an ANOVA and found a significant effect of distance ($F(1, 14) = 14.725, p = .002$) and a significant effect of timing ($F(1, 14) = 5.671, p = .032$). The interaction was not significant ($F(1, 14) = 1.028, p = .383$). When we expressed the effect as a percentage of the distance between the hands (rather than cm), we found a statistical trend for the significant effect of timing ($F(1, 14) = 3.640, p = .077$) and a statistically significant effect of distance ($F(1, 14) = 14.520, p = .002$). The interaction between timing and distance was not significant ($F(1, 14) = 1.044, p = .324$).

In the planned pairwise comparisons, we found a significant difference between the synchronous and asynchronous conditions, both at the 12 cm distance ($t = 3.014, df = 14, p = .009$) and at the 27 cm distance conditions ($t = 3.045, df = 14, p = .009$). These results suggest that the subjectively experienced illusion was also reflected in the proprioceptive drift toward the model hand at both the 12 cm and the 27 cm distances (Fig. 7b).

6. Discussion

The present results show that there are spatial constraints for how close the participant's hand and the model hand must be placed for the moving rubber hand illusion to be elicited. In line with previous observations on the classical illusion (Lloyd, 2007; Preston, 2013), we observed that with increasing distance, the moving version of the illusion becomes weaker. This was seen both in the questionnaire data and in the proprioceptive drift data. Interestingly, whereas sense of ownership decreases or is abolished with increasing distance, sense of agency over the hand was present at all of the distances when the fingers moved synchronously. These observations are interesting for two reasons. First, they suggest that ownership in the moving rubber hand illusion paradigm corresponds to the same process as ownership in the classical rubber hand illusion paradigm because both obey a similar spatial distance rule. Second, they provide further evidence that ownership and agency constitute two different processes due to the spatial rule being exclusively applied to ownership (Kalckert & Ehrsson, 2012). Finally, our data revealed the unexpected and interesting observation that the moving rubber hand illusion might obey a slightly narrower spatial constraint than the classical version of the illusion: whereas the classical version of the rubber hand illusion was elicited at both the 12 cm and the 27 cm distances, the moving rubber hand illusion was only robustly elicited at the closest distance of 12 cm. This pattern was observed both in the questionnaire data and in the proprioceptive drift experiments. We discuss these latter results in light of their potential underlying mechanisms and propose the hypothesis that efference copy signals produced by the active finger movements might cause the spatial window of visuo-somatic integration to shrink when compared with the relaxed hand state (see below).

Our observations comply with the idea that there are general spatial limits to the underlying mechanisms of the rubber hand illusion. Our study is the first that examines the spatial constraint of the illusion in the vertical plane and the first to examine this constraint for the moving version of the rubber hand illusion paradigm (in any plane). Lloyd (2007) found that the classical illusion declines already at the 27.5 cm distance, a distance we used here as well. In her study, the model hand was positioned medially to the participant's right hand and subsequently tested at distances up to 67.5 cm in the horizontal plane. The spatial arrangement of the hands in her study resulted not only in varying the distance between the hands, but it also varied in the congruency between the posture of the rubber hand and the posture of the participant's arm. When the rubber hand was positioned to the left, further away from the participant's hand, the posture of the rubber hand also became increasingly rotated and, thus, different from the orientation of the real hand (compare Lloyd, 2007; Fig. 1). Thus, in principle, both the distance between the hands and the changes in the rubber hand's posture could have contributed to the observed effect. In the present study, this potentially confounding factor was not an issue because the model and the real hand were always oriented in the same direction. In apparent contrast to our observation, however, Zopf et al. (2009) found no difference in illusion strength when the hands were placed either in *close* (15 cm) or *far* (45 cm) positions from one other, although the lack of difference between the synchronous and asynchronous conditions at the closest distance makes it difficult to interpret these results (Zopf et al., 2009). Preston (2013) found that the distance between the rubber hand and real hand, as well as the relative distance between the model hand and the trunk, is important in modulating the illusory experience. However, this factor cannot bias the present results because the distance to the trunk was identical across conditions. In sum, the present study is in agreement with previous studies that show an effect of distance between the real hand and the rubber hand in the ownership illusion (Lloyd, 2007; Preston, 2013).

In light of this discussion, a couple of more studies are worth mentioning. Armel and Ramachandran (2003) placed the rubber hand at a distance of 91 cm from the participants and concluded that the illusion could still be induced, i.e., at a distance that was much greater than the furthest distance tested in the present study (see their Experiment 3). However, the results presented in the figures of this paper actually show that for both the subjective ratings and the skin conductance response triggered by a simulated injury of the rubber hand, there is a substantial reduction in effect sizes when comparing the far distance condition to the close distance condition. The subjective ratings were actually significantly lower in the far condition. A further observation that is informative in this regard and consistent with our results comes from the "invisible hand illusion" (Guterstam, Gentile, & Ehrsson, 2013), which can be seen as a counter-intuitive variant of the rubber hand illusion paradigm: despite the fact that no rubber hand is visible here and instead the empty space in front of the participants is "stroked," participants experience the illusion of sensing an owned invisible hand in the location where they see the

strokes occurring. When the stroking is viewed to occur at a distance of 75 cm from the participant, i.e., outside peripersonal space, this illusion could not be elicited, consistent with the present findings and the findings of Lloyd (2007).

As described above, a notable difference between the present paradigm and the ones used in previous literature is that we manipulated the relative distance between the hands in the vertical plane rather than in the horizontal plane (Lloyd, 2007; Preston, 2013; Zopf et al., 2009). Although the spatial arrangement of the hands used in the present paradigm deviates from the classical description of the rubber hand illusion (Botvinick & Cohen, 1998), subsequent studies have shown that this illusion can be induced when the rubber hand is placed above the real hand in a vertical arrangement (Bekrater-Bodmann, Foell, Diers, & Flor, 2012; Ehrsson et al., 2004; Haggard & Jundi, 2009; Kalckert & Ehrsson, 2012, 2014). A study on human position sense has shown that visual and proprioceptive information is weighted differently in different parts of space during the process of localizing the hand (van Beers, Wolpert, & Haggard, 2002). Therefore, depending on the specific plane (vertical vs. horizontal), the visual and somatosensory information might be weighted differently and, consequently, might differently affect the resolution of the multisensory conflict that leads to the rubber hand illusion in different parts of space. Thus, we cannot assume that the spatial rule will be absolutely symmetric in all dimensions of space, and this is a further reason why we cannot directly compare the present results to those of Lloyd (2007): for example, the diminishing classical rubber hand illusion that she observed at the 27.5 cm distance, a distance at which we did not observe a reduction in illusion strength. Further studies are needed to directly compare the effect of the relative distance between the rubber hand and the real hand in different parts of space and to determine how this affects the different versions of the rubber hand illusion.

Thus, the overall picture that emerges from the previous studies and the present experiments on the moving rubber hand illusion is that the perceptual processes that underlie the illusion obey a spatial distance rule. This rule bears similarity to principles found in multisensory integration (Holmes & Spence, 2005; Stein & Stanford, 2008) and in the concepts of peripersonal space and perihand space. When the model hand is moved outside the peripersonal space, a vivid illusion seems to not be inducible (Guterstam et al., 2013), even when taking into account the observations made by Armel and Ramachandran (2003). It is noteworthy that recent experiments with slowly elongating virtual arm illusions do not refute this conclusion because then the reaching space (and most likely the peripersonal space) is also slowly expanding as the arm is being elongated (Kilteni, Normand, Sanchez-Vives, & Slater, 2012). Importantly, in the present study, the model hand was never moved outside the peripersonal space and was always kept within reaching distance. This means that the spatial effects that we observed here most likely relate to perihand space, which is the distance between the hands, as defined in a spatial coordinate system centered on the hand and extending to approximately 30 cm from it (Brozzoli, Gentile, & Ehrsson, 2012; Lloyd, 2007). Taken together, these observations corroborate the idea of a close link between the mechanisms of multisensory integration, peripersonal space, perihand space and the feelings of body ownership (Brozzoli et al., 2012, 2013; Makin, Holmes, & Ehrsson, 2008).

Intriguingly, our questionnaire data and results from the proprioceptive drift experiments collectively suggested that the moving rubber hand illusion might obey a narrower spatial rule than the classical version. Already at the distance of 27.5 cm, participants typically did not affirm ownership of the model hand in the synchronous finger movement condition, which was different from the classical version of the illusion where participants, on average, still affirmed ownership at this distance. Ownership was not fully abolished until the furthest distance of 43 cm. We also observed that significantly fewer participants affirmed ownership in the moving rubber hand illusion at the 27.5 cm distance than were found to affirm ownership in the classical version of the illusion at this distance. What could be the reason for this possible difference in the extent of the spatial constraints? In principle, this observation could be ascribed to differences in the kinds of somatosensory information involved or be related to the efference copy mechanisms that are associated with active voluntary movements. In the classical rubber hand illusion, the participants observe a small physical object moving in the perihand space and touching the skin of the rubber hand while the participants' hand is stroked in the same way. The illusion induced in this way most likely depends heavily on the integration of visual information and touch, and also on the sight of the external object moving in the perihand space in a particular trajectory (Guterstam et al., 2013). By contrast, in the moving rubber hand illusion, the somatosensory feedback involves a multitude of proprioceptive and kinesthetic information from skin stretch, muscle spindles, joint receptors and others (Edin & Abbs, 1991; Edin & Johansson, 1995; Proske & Gandevia, 2012), and the visual stimulus is that of a moving finger. These differences in the type of the available sensory information could possibly explain the apparent differences in the spatial rule observed here. It could be the case that the integration of visuo-tactile vs. visuo-motor information has different spatial limits in which multisensory neurons can effectively integrate these different pairings of sensory inputs. A second possibility could be that the efferent information associated with the voluntary motor commands (most likely efference copy signals) could influence the spatial window of the integration of the visual and somatic signals. Due to such a theorized reduction in the spatial window of integration, the somatic and visual stimuli would need to occur closer in space for effective multisensory integration and perceptual binding to occur. Although this is speculative and the exact mechanism is not known, we know from the previous literature that efference copy mechanisms do change the central processing of somatosensory information through comparator mechanisms (Bays & Wolpert, 2006; Johansson & Flanagan, 2009) and that they can influence performance in visuo-motor congruency detection tasks that involve finger movements (Shimada, Qi, & Hiraki, 2009). It has also been shown that firing rates and response features, such as tuning width and preferred direction of neurons in the macaque parietal cortex, differ when comparing active and passive movements, possibly driven by efference copy mechanisms (Gabel, Misslisch, Gielen, & Duysens, 2002; Klam & Graf, 2006). Future experiments are needed in order to address these questions. In particular, studies that directly compare the moving

rubber hand illusion during active and passive movements across distances in order to evaluate how efferent signals modulate the multisensory processes that underlie the rubber hand illusion are needed.

Whereas the spatial separation of the two hands influenced sense of ownership, this was not the case for sense of agency. Participants had a strong experience of agency during synchronous movements at all of the three distances. This is in line with our previous observation that ownership and agency do not always have to “go hand in hand,” but they can be dissociated (Kalckert & Ehrsson, 2012): at the closest distance, participants experienced a sense of ownership and a sense of agency over the moving hand; whereas at the 43 cm distance, they only sensed agency over the hand, and the hand no longer felt as part of one's own body. This highlights that the mechanisms for the generation of sense of agency are not confined to peripersonal space and body-centered coordinate systems, but they can most likely apply equally to any feedback that originates from the external world at any distance from the body. In line with the view that a match between a prior intention to move and the actual sensory feedback from the movement is a crucial factor for sense of agency to arise (David et al., 2008; Synofzik, Vosgerau, & Newen, 2008), we observed that agency ratings were always significantly higher after synchronous feedback than after asynchronous feedback in the movement conditions. Moreover, agency was always rated significantly higher after the active movements than after the visuo-tactile stimulation condition when the hand was passive. This is in line with the idea that the intention to move is also an important factor that drives one's sense of agency (Haggard, 2005).

Many observations, such as the spatial and temporal rules of the rubber hand illusion, suggest that the underlying mechanisms of the illusion relate to principles that are found in multisensory integration (Ehrsson, 2012; Holmes & Spence, 2005; Stein & Stanford, 2008). Neurophysiological recordings in the non-human primate have found multisensory neurons in various regions, such as the premotor and posterior parietal cortex, which integrate both visual and tactile information (Avillac, Denève, Olivier, Pouget, & Duhamel, 2005; Duhamel, Colby, & Goldberg, 1998; Graziano, Hu, & Gross, 1997; Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981a,b). These bimodal neurons integrate stimuli in a body part specific manner so that, for example, a neuron that responds to touches to the hand also responds to a visual stimulus presented near the hand but not near other body parts. Interestingly, when the hand changes its position, the visual receptive field of the neurons moves along with the hand, which makes it seem to be anchored to the body part (Graziano et al., 1997). Graziano, moreover, described neurons in the monkey premotor cortex (Graziano, 1999) and posterior parietal cortex (Graziano, Cooke, & Taylor, 2000) that integrate visual and proprioceptive information from the hand on the basis of their tonic background discharge rates. It seems likely that those neurons with overlapping arrangement of visual and tactile receptive fields that are confined to the immediate space around the body are involved in the multisensory representation of the body, the space near the body, and limb ownership illusions (Brozzoli et al., 2012; Ehrsson, 2012; Gentile et al., 2013). Recent evidence from functional imaging supports the existence of similar mechanisms in the human brain. The ventral premotor cortex and the posterior parietal cortex respond to congruent visuo-tactile stimulation on the real hand (Gentile, Petkova, & Ehrsson, 2011; Gentile et al., 2013) and are sensitive to visuo-proprioceptive congruency of seen and felt arm orientations (Gentile et al., 2013), which is what one would expect from the non-human primate literature. fMRI activity in these areas also reflects the rubber hand illusion (Brozzoli et al., 2012; Ehrsson et al., 2004) and the presentation of a visual stimulus near an owned rubber hand (Brozzoli et al., 2012). Thus, our interpretation is that the spatial distance rule in the rubber hand illusion paradigm (the moving version included) relates to the spatial constraints of receptive fields of multisensory neurons in premotor and intraparietal cortices that represent the limbs in space.

In conclusion, the present study extends our knowledge about the moving rubber hand illusion paradigm into the spatial domain by demonstrating that the moving rubber hand illusion obeys a spatial rule that is similar to the spatial rule in the classical version. This corroborates the view that multisensory processes related to perihand space are involved in the moving rubber hand illusion (Kalckert & Ehrsson, 2012, 2014) and that these processes are considered to be present in the classical version of the illusion as well (Brozzoli et al., 2012; Lloyd, 2007). Moreover, the present results provide further evidence that supports a dissociation of ownership and agency in the rubber hand illusion paradigm (Kalckert & Ehrsson, 2012) by showing that only the former type of self-related experiences is constrained by the rubber hand's distance from the body.

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